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Sex differences in nest construction incubation and parental behavior in captive American golden eagles (Aquila chrysaetos)

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SEX DIFFERENCES IN NEST CONSTRUCTION, INCUBATION, AND PARENTAL BEHAVIOR IN CAPTIVE AMERICAN GOLDEN EAGLES (*AQUILA CHRYSAETÖS*)

By

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ABSTRACT

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Sex Differences in Nest Construction, Incubation, and Parental Behavior in Captive American Golden Eagles (Aquila Chrysaetos) (64 pp.)

Director: Donald A. Jenni

An eleven-year study of captive golden eagles was made in order to describe and understand the differences in the roles of the sexes during reproduction. Pair bonding, nest construction, incubation, and parental behavior were described. Two pairs of eagles were maintained in a large aviary. In addition to direct behavioral observations, egg temperatures and nest attendance were recorded with electronic and photographic equipment. Pair bonding, which took six years for one pair, is necessary for successful copulation. The male performed 90 percent of nest construction, the female performed 82 percent of incubation. Both birds maintained constant egg core temperatures of 32.8°C. The female provided almost all direct parental care, but the male brought food to the nest for both the female and the chick. The male was most active in nest defense. His aggression peaked just after egg hatching. Pairs successfully fostered eaglets and red-tailed hawks, but failed with a great horned owlet. One pair reproduced successfully in captivity and fledged an eaglet.

ACKNOWLEDGMENTS

It has only been through the effort of my entire family (John, Margaret, Karen, and Johnny Craighead) in housing, caring for and feeding a backyard full of eagles, and many other wild birds, that I had the opportunity to make this study. There is no vacation from the responsibility of caring for captive birds, and procuring food for twelve eagles is a time-consuming and often expensive chore that the entire family and many friends shared with me. My father has constantly guided and helped in this investigation and, were it not for his parental pushing, I would never have finished it. I thank John Mitchell for encouragement and constructive editing. Final thanks to my committee; Dr. I. Joseph Ball, Dr. B. Riley McClelland and to Dr. Donald A. Jenni, chairman. Dr. Jenni kindly accepted me into his graduate program and has been supportive and helpful throughout. Financial support was provided by the Wildlife-Wildlands Institute.

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CHAPTER I

INTRODUCTION

The nesting strategy of the golden eagles (Aquila chrysaetos) is typical of large raptors. The golden eagle is monogamous, and nest construction, incubation, and parental behavior are shared, but not necessarily equally, by both sexes (Bent 1973, Kendeigh 1952). The importance of sexual variability in nesting strategies has been detailed for some species, particularly those that show unusual behavioral roles such as polyandrous jacanas (Jacana spinosa) (Jenni and Betts 1976), a polyandrous trio of Harris hawks (Parabuteo unicinctus) (Mader 1979), and polygamous harrier hawks (Circus cyaneus) (Balfour 1957). However, there is only sketchy and sporadic mention in the literature of the relative behavioral roles of male and female golden eagles during the breeding cycle.

Both male and female golden eagles added material to their nest in the Topeka Zoo (Kish 1970). A female eagle took the greater share of the incubation duties, but was attended by the male who brought her food. The female incubated by night and the male relieved her for short periods during the day. One pair copulated occasionally throughout the incubation period and for two weeks following hatching. Only the male refurbished the nest after incubation had begun (Kish 1972). During a two-day watch

both members of a pair returned to the nest with food (Gilbert 1934).

Similar observations and notes on other hawks and eagles suggest that gross aspects of nesting behavior are relatively uniform in the Accipitridae. The female of a breeding pair of white-tailed sea eagles (Haliaeetus albicilla) at the Kansas City Zoo incubated with the first egg and performed 80% of incubation (Wylie 1973). The male attended the eggs only during the daytime when the female was feeding or preening. In a pair of captive long-legged buzzards (Buteo rufinus), the female incubated. The male relieved her only when she left the nest to feed (Mendelssohn and Marder 1970). However, the male took on a larger share of incubation with successive annual broods and, by the 9th or 10th year, incubation was shared equally by both sexes. The male carried food to the nest, but only the female fed the young. The female of a pair of breeding white-tailed sea eagles at the Vienna Zoo, performed most of the early incubation, and did most of the feeding of the young. In all species of Haliaeetus both sexes participate in nest building. However, a captive female Steller's sea eagle (Haliaeetus pelagicus) was observed nest building in February; the male did not participate until April (Dathe 1970). A male captive Harris hawk sat on the edge of the nest when the female left, but never incubated. He brought food, but the female fed the young (Gale and White 1970). A male bald eagle (Haliaeetus leucocephalus) at the National Zoological Park in Washington, carried the majority of sticks to the nest platform while the female arranged them and lined the nest

with grass. The female incubated 80% of the time, and always from dusk until dawn and performed the brooding, while the male only carried food to the nest (Johnson and Gayden 1975). A female harpy eagle (Haliaeetus haliaeetus) at the Los Angeles Zoo assumed most of the incubation responsibilities and the male fed her at the nest, when she did leave the nest to feed, the male incubated and turned the eggs. The male spent less than one hour per day incubating and, though he brought food to the nest, was never observed feeding the young. He performed most of the nest repair work (Todd and Meachan 1974). Five nests observed by Brown (1976) revealed that at one nest a female crown eagle (Stephanoaetus coronatus) performed all incubation, but at four others the male shared incubation. The female of a breeding pair of Griffon vultures (Gyps fulvus) at La Fleche Zoo, incubated throughout the night and was relieved by the male only in the morning when she drank, bathed, and preened. Both the male and the female left the eggs in the evening to feed. In a second pair the male performed the majority of incubation (Bouillault 1970).

It is evident from the literature that in eagles and related birds the role of the sexes varies, but the biological significance is not well understood. To further understanding, I made observations on the comparative roles of male and female captive golden eagles. My major objectives were to describe pair bonding, nest construction, incubation, and parental behavior, with special emphasis on the relative roles of the sexes.

CHAPTER II

MATERIALS AND METHODS

Study Area and Facilities

The study site was on 2.5 ha of privately owned property adjacent to Upper Miller Creek Road, Missoula County, Montana. A small gully, approximately 25 m wide with overmature ponderosa pine (Pinus ponderosa) provided protection for the birds. The pines shaded the eagles during hot summer months, and the gully deflected winter winds and shielded them from human disturbance.

Two aviaries 7.3 x 11 x 4.6 m each were constructed of chain-link fence and nylon fish netting. The house-like aviaries had side walls of 2.4 m high chain-link fence with roofs and gables of 5.7 cm mesh nylon fishing net. Perches of various heights (0.5-3 m) and several tree snags were anchored inside the aviaries. A 3.6 m^3 covered plywood nesting box was located 0.5 m above the ground against one wall of each aviary (Fig. 1). The side of each nesting box facing into the aviary was left open. A 1 m diameter metal pan 15 cm deep provided drinking and bathing water.

During the nesting season, freshly-killed ground squirrels (Spermophilus columbianus) were placed just inside the aviary door as a source of food for the eagles. During nest construction and incubation 2-3 squirrels were fed to the pairs each day. After hatching 3-6 squirrels were fed each day. The number of squirrels was adjusted to prevent accumulation of uneaten food.

Figure 1. Aviary for housing golden eagles.

The Birds

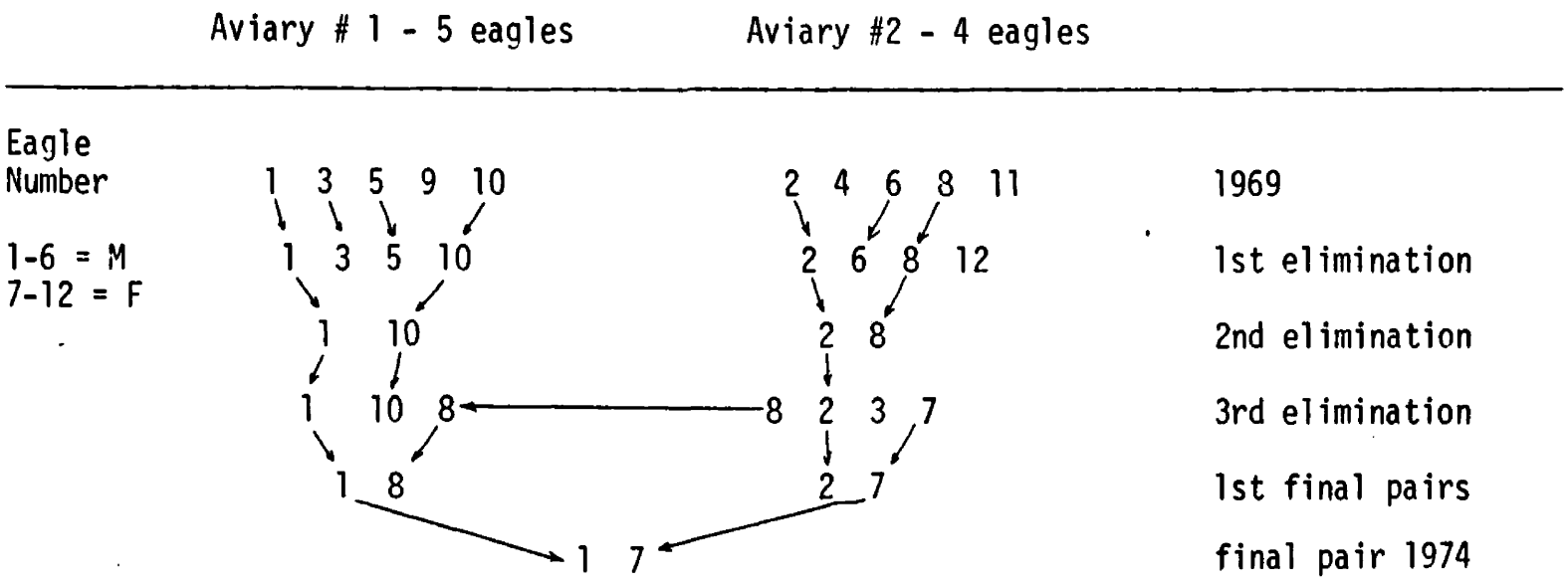
Twelve eagles (four healthy and eight injured) were available from previous studies conducted by the Montana Cooperative Wildlife Research Unit at Missoula, Montana (Table 1). The injured birds, with the exception of one female, had been surrendered to the USFWS suffering gunshot wounds, trap injuries, or poisoning, and were being rehabilitated for release to the wild. Four of the eagles, including one female with an injured wing, were acquired as nestlings. All eagles were weathered, handled, fed, manned, and trained using traditional falconry techniques (Craighead and Craighead 1950).

In 1969, to begin establishment of nesting pairs, I introduced successively over a period of several months two to five eagles into each of the two aviaries. As agonistic behavior developed, seemingly incompatible birds were transferred from one aviary to the other or removed from the experiment. Progressive elimination resulted in one apparently compatible pair in each aviary (Fig. 2). The birds in aviary #2 were raised from nestlings and flown in the manner of falconry for many years prior to this experiment. Both members of this pair were frequently released to fly and hunt together for 1-4 hours approximately every other day during 1971-73. Though the pair seemed compatible throughout most of the year, the female became very aggressive toward the male during the spring. The birds were judged incompatible and separated, following the spring of 1973. The pair in aviary #1 provided research data from 1969-1974, when the male died. The female was then paired with the

Table 1. Potential and actual experimental Golden Eagles in 1969.

Bird No.	Sex	Age	Name	Condition
1	M	9 years	Ion	Healthy
2	M	11 years	Rana	Healthy
3	M	Adult	--	Wing injury/recovered
4	M	Adult	--	Wing injury/recovered
5	M	Adult	--	Leg injury/recovered
6	M	Adult	--	Poison/recovered
7	F	4 years	Lame Wing	Wing injury
8	F	5 years	Chastity	Healthy
9	F	Adult	--	Wing injury/recovered
10	F	Adult	--	Wing injury/recovered
11	F	Adult	--	Porcupine quills/recovered
12	F	Adult	--	Sick/recovered

Figure 2. Flow chart of pair bonding elimination procedure.


Aviary # 1 - 5 eagles
Aviary #2 - 4 eagles
Eagle Number
1-6 = M
7-12 = F
1 3 5 9 10
2 4 6 8 11
1969
1 3 5 10
2 6 8 12
1st elimination
1 10
2 8
2nd elimination
1 10 8
8 2 3 7
3rd elimination
1 8
2 7
1st final pairs
1 7
final pair 1974

male from aviary #2. Data was gathered on this final pair subsequent to 1974.

Data Collection

Observations of nesting activities were made through a one-way window in a blind placed outside the aviary 5 m from the nest platform. Observations were also made from the window of a house 65 m from the nesting platform. For detailed description of the blind see Ellis (1979). Eight power binoculars were used when necessary, but most observations were at close range. While in the blind I was equipped with a Bolex 16mm movie camera with a 12-85mm zoom lens, and several SLR cameras and lenses. Interesting and unusual events and behaviors were detailed chronologically in a journal maintained each year during the nesting period.

A telemetering dummy egg (Ellis and Varney 1973, 1974a, 1974b) was used in 1974 to gather continuous incubation temperatures and nest attendance data over a 10 day period. During this period, and for 10 additional days, time lapse pictures recorded specific behavior, nest attendance, and activity patterns. One exposure was recorded per minute with a Super 8mm movie camera with automatic aperature control. A photoelectric switch activated the system at dawn and deactivated it at dusk. To automatically record egg incubation temperatures, an egg shell was cut in half and fitted with a transmitter equipped with two temperature probes (Varney and Ellis 1973). The egg was filled with paraffin having a specific heat of 0.63 cal/gram/C^{o}. This approximated the egg albumin value of 0.77

cal/gram/C^{o} for a natural egg (Romanoff and Romanoff 1949). The egg was temperature-calibrated within $\pm$0.2^{o}C to permit accurate assessment of the temperatures during incubation. Egg shell and egg core temperatures were transmitted to and recorded on a Rustrak strip chart recorder. Some behaviors and attendance of the sexes was also recorded on the strip chart (Fig. 3).

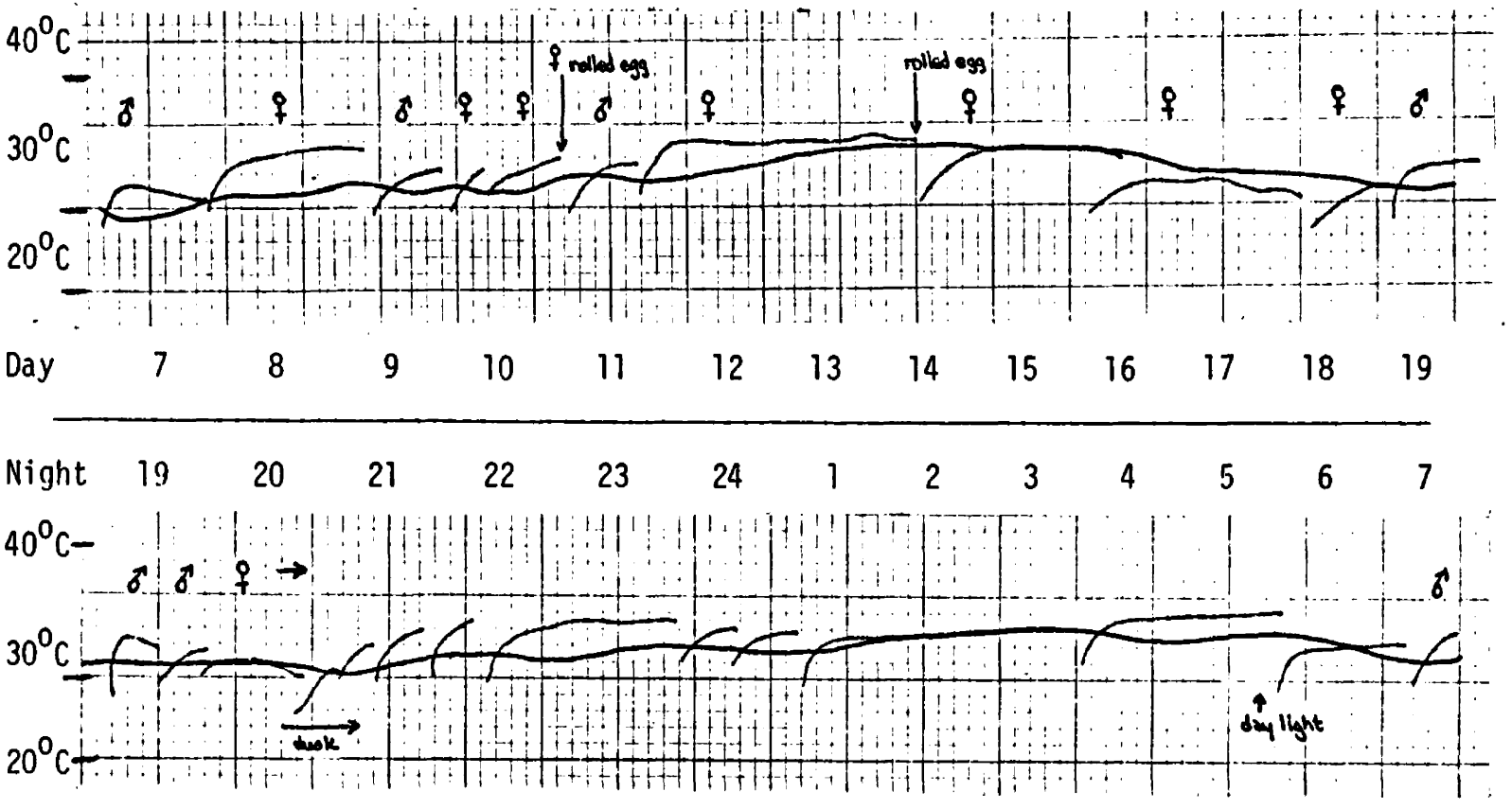
Fostering and Cross-Fostering

Foştering refers to a pair of adults raising the offspring of another of their own species. Cross-fostering refers to a pair of adults accepting and raising the young or eggs of a different species. These two techniques permitted nesting eagles with infertile eggs to complete the nesting sequence. This strategy allowed the pair to gain parental experience.

Terminology

Action patterns such as incubation, brooding, or feeding may occur in "bouts" or "sessions." Bout describes when one of the adult eagles persisted at an activity uninterrupted. For example, a bout of incubation would end when the bird stood to roll the egg. A session is a sequential set of bouts of one behavior uninterrupted by bouts of other behavior. A session of incubation bouts ended when one bird was relieved by the other. Nest attendance is considered time spent on the nest platform.

Figure 3. Incubation temperatures as recorded on Rustrak Strip Chart for 24-hour period, 1974.


40°C
30°C
20°C
♀ rolled egg
rolled egg
Day 7 8 9 10 11 12 13 14 15 16 17 18 19
Night 19 20 21 22 23 24 1 2 3 4 5 6 7
40°C
30°C
20°C
dusk
day light
Solid core temperature
Broken shell temperature

CHAPTER III

RESULTS

The Formation of Pairs

Of the 12 eagles available for study, only birds captured as nestlings formed pair bonds, viz., female #7 and males #1 and #2 (Fig. 2). A fourth eagle, female #8, was raised in captivity, but had imprinted on me or formed a pair bond with me or both and remained unreceptive to male golden eagles. When I moved in sight of her she emitted a quiet "whistle-chirp" greeting call. She allowed me to sit next to her, to touch her and to preen her feathers. Males #1 and #2 were both handled extensively for eight years prior to the study, yet showed no signs of a continued allegiance to me. Female #7 was handled very little, and was essentially untamed. The remaining eagles, all captured as adults, were apprehensive in captivity, and did not seem to respond during the nesting session.

Female #7 was four years old when first placed in the aviary in 1969; male #2 was eight. In 1973 they established a pair bond and began courting and nest-building activities. The development of the pair bond between these two birds was subtle and occurred over many months. During the summer of 1972 their behavior changed from mild avoidance to placid acceptance of one another. By fall, the birds perched in the same vicinity and finally, on the same perch. While perched together in late winter, the birds touched beaks and "nibbled" one another's contour feathers at the base of the neck and shoulders. The pair constructed an elaborate nest during the spring

of 1973 and laid an egg, but not until 1974 did the 13-year-old male attempt to copulate with the 9-year-old female. Unfortunately, during the summer following establishment of the pair bond, the male contracted aspergillosis and died. To continue experimentation, the 14-year old male #1 from aviary 2 was introduced into aviary 1. Agonistic behavior was minimal between these birds and, by February, they appeared to be bonded and cooperated in construction of a nest.

Copulation

From 1974-1979 up to three copulation attempts were observed each spring, but none appeared to be successful. During 10 hours of observation in 1980, the pair was observed to copulate 7 times over a three week period just prior to egg laying. No copulations were observed during incubation. The eggs of the first clutch of 1980 broke; a second clutch was laid 15 days later. Two copulations were observed between the loss of the first clutch and the laying of the second clutch. The copulations of 1980 were of greater intensity and duration than those observed during the 1974-1979 period, and subsequently proved to be successful. Their copulatory behavior was similar to that described by Ellis (1979). The copulations in 1980 occurred on the ground and lasted from 5-30 sec. The female emitted high pitched squawks or whines which were unique to the copulatory act.

Nest-building

By February of every year both birds frequently picked up sticks and showed a definite propensity to nest build (Figs. 4 and 5).

Figure 4. Nesting chronology of captive golden eagle.

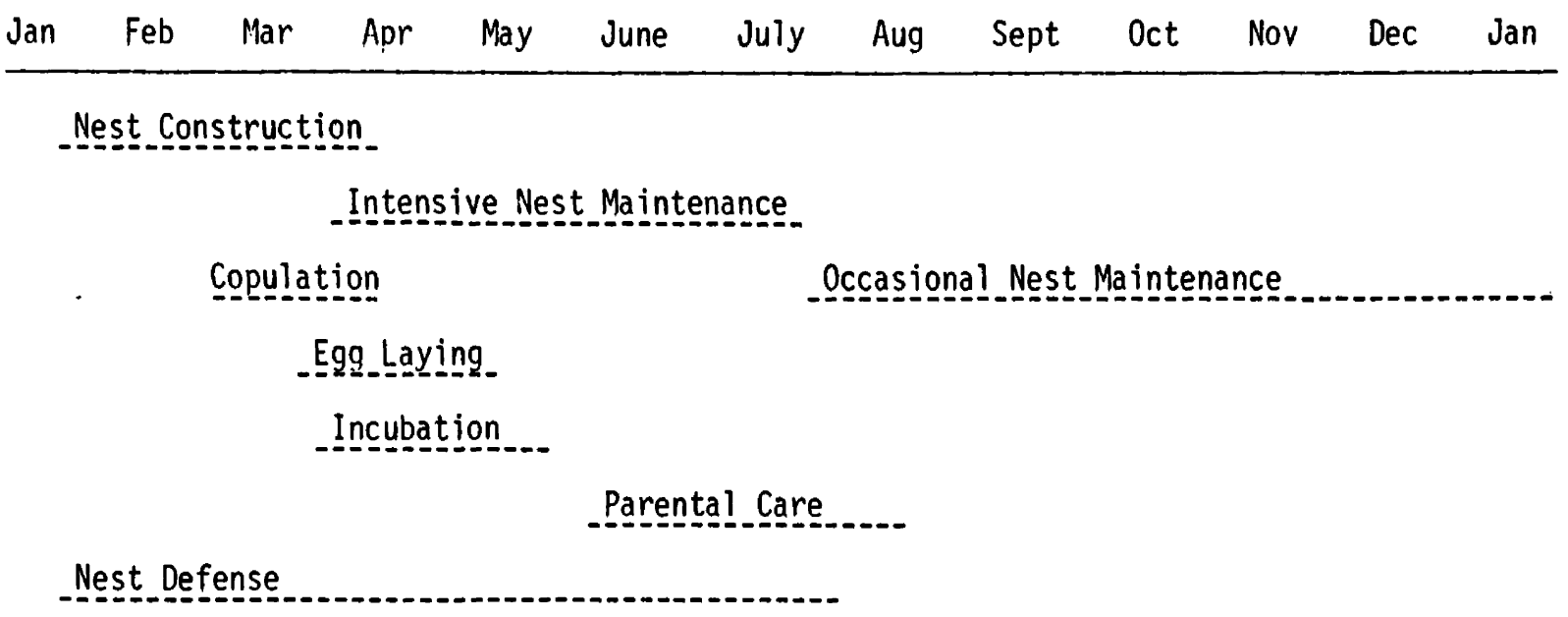
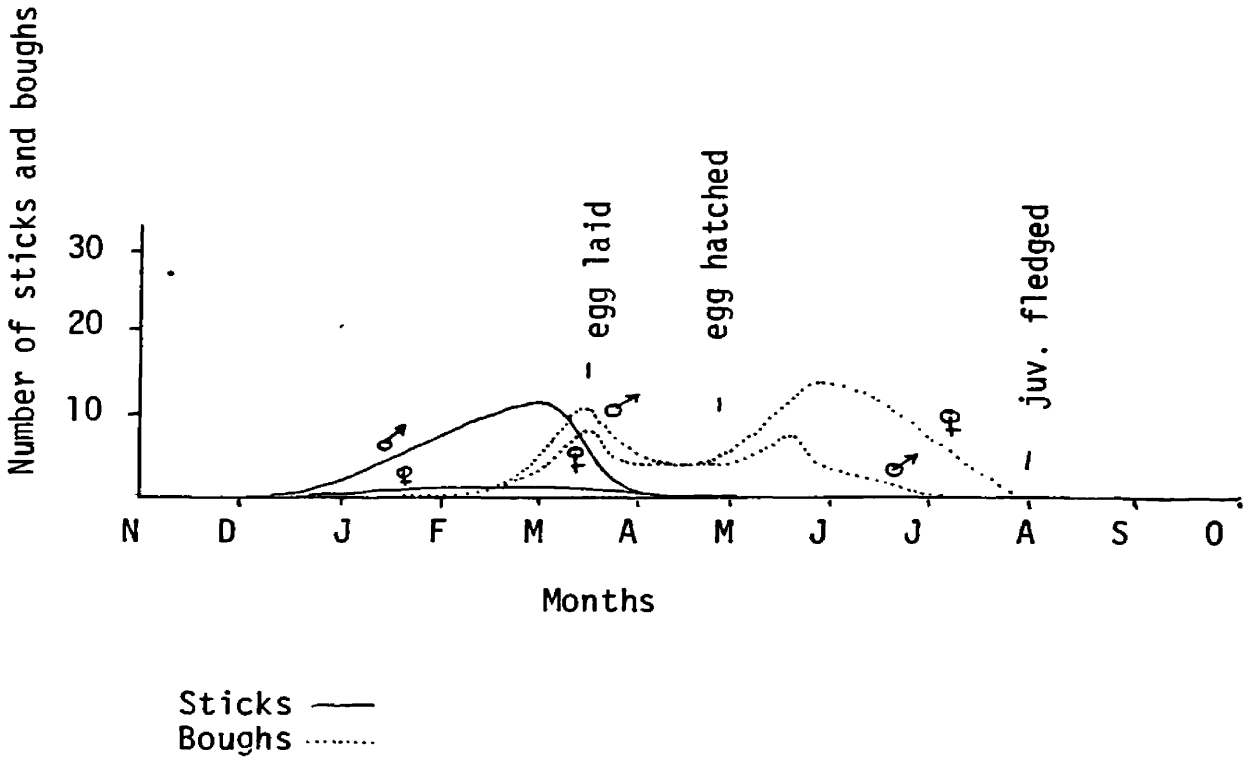

Jan
Feb
Mar
Apr
May
June
July
Aug
Sept
Oct
Nov
Dec
Jan
Nest Construction
Intensive Nest Maintenance
Copulation
Occasional Nest Maintenance
Egg Laying
Incubation
Parental Care
Nest Defense

Figure 5. Average number of sticks and boughs eagles brought to nest.


Number of sticks and boughs
30
20
10
N
D
J
F
M
A
M
J
J
A
S
O
Months
egg laid
egg hatched
juv. fledged
♂
♀
Sticks
Boughs

A variety of branches, twigs, green boughs, and grass was introduced into the aviary and the birds constructed a nest using these materials in that order. The eagles spent much time and effort placing and arranging each branch on the nest. The completed nest measured about 1 m in diameter by 0.3 m high. Though much new material was added each season, the nest did not grow over the years. The nest was used as a feeding and perching platform during the non-nesting periods and considerable nesting material was dislodged.

The males performed most of the nest construction. Nest-building began by the first week of February each year and continued until the first egg was laid. A continuous supply of nest material was available to the birds. Data from 1979 typifies nest construction. During the nesting season the pair carried approximately 900 branches and boughs to the nest. During the first week of March, the male carried 90 branches and the female ten branches to the nest platform. On warm sunny days the pair carried as many as 20 branches to the nest, but during inclement weather they often carried no more than one or two branches. After egg-laying, the male occasionally placed green boughs over the pair's mutes and old food carcasses. The addition of boughs around the edge of the nest also helped maintain a deep nest cup which sheltered the egg (Ellis 1979).

After the last infertile egg broke on 8 June, I air dried and weighed the 1979 nest material. Twenty-three pounds of material had been carried to the nesting platform, with an additional five pounds carried to an adjacent, 1 m^2 perching platform. An

additional 45 pounds of nesting material had accumulated on the ground at the base of the nesting box. This material had been either carried to the nest and dislodged or had been dropped as the birds attempted to maneuver it into the nest. Several large branches (1 m by 3-5 cm) had been dragged to the base of the nest box, but the birds were unable to lift them to the nest. Because the small size of the aviary prevented the birds from flying with large sticks they grasped them with one foot and hopped on the other while using their wings and tail for balance. The birds dragged the sticks to the base of the nest box where they were discarded.

They carried light-weight materials up to 80 cm in length to the nest in the beak. The material usually extended at right angles to the bird's mid-line. To prevent the material from hitting obstacles en route to the nest, the birds turned, rolled and yawed their heads. On the nest with the stick held in its beak, the eagle flexed the ankles, knees, and hips, leaned forward extending its neck and head forward and down, and while rolling and yawing its head, poked with the stick until it was satisfactorily placed. When a bird returned to the nest with a small green bough, in its beak, it simply leaned forward and dropped the bough onto the nest matrix. It would regrasp the bough in its beak, and either throw it to one side or take several steps across the nest to drop it once more. The bough might be picked up and dropped in this manner a dozen times before it was abandoned. Bunches of grass were grasped in the talons of one foot, flown to the nest, and arranged in the same manner as were boughs.

Sticks and boughs were placed in a roughly circular area about 1 m in diameter. The sticks were arranged perpendicular to the nest radius. When the nest approached a uniform height of 8-10 cm, a nest pocket was excavated in the center by both birds. A bird leaned forward, transferring most of its body weight to the anterior portion of the breast. Its beak was frequently in contact with the nest platform. It then drooped its wings slightly at the elbow (possibly for balance and support), thrust its body forward in short, abrupt motions by pushing backwards with the legs. By pushing sticks forward with the breast and backward with the feet, the bird gradually created a broad depression in the center of the nest. As the depression was formed, the birds lined it with fine twigs, boughs, and, lastly, grass. The male performed this behavior more frequently than did the female. The action pattern occurred at intervals throughout each day, and most frequently during the two weeks prior to egg laying. After lining the nest, the eagles completed the nest cup. A bird leaned forward, rested on the upper margin of its breast, drooped its wings and very rapidly paddled its feet, while rocking from side-to-side, movements termed "foot-digs" and "rock-downs", respectively, by Ellis (1979). Repetition of this behavior pattern formed a pocket in the grass lining approximately 5 cm wide and 5 cm deep. Shortly after formation of the cup, the female laid the first egg.

Egg-laying

Nest building ended each year when the female settled over the nest pocket as if incubating; generally she laid the first egg within the next 12 to 36 hours. The mean dates for laying the first and second egg were 26 and 30 March, respectively (Table 2). In 1973, the female laid only one egg. The eggs of the first clutch of 1980 broke during a period of disruption. Fifteen days later the female laid the first egg of a second clutch.

The date and time of laying for the first egg of each clutch was accurately determined each year. Because the pair began sitting on the egg immediately, precise verification of the time of laying of the second egg was difficult. The estimated average interval between the laying of the first and second eggs was 36 hours (Table 2).

The first egg, which was laid in 1973, was heavily pigmented. With each successive year the eggs became less pigmented, those laid in 1979 were nearly white. The only exception to this was the second egg of the 1980 season which was heavily pigmented. The first egg of each clutch was always more pigmented than the second egg (Fig. 6).

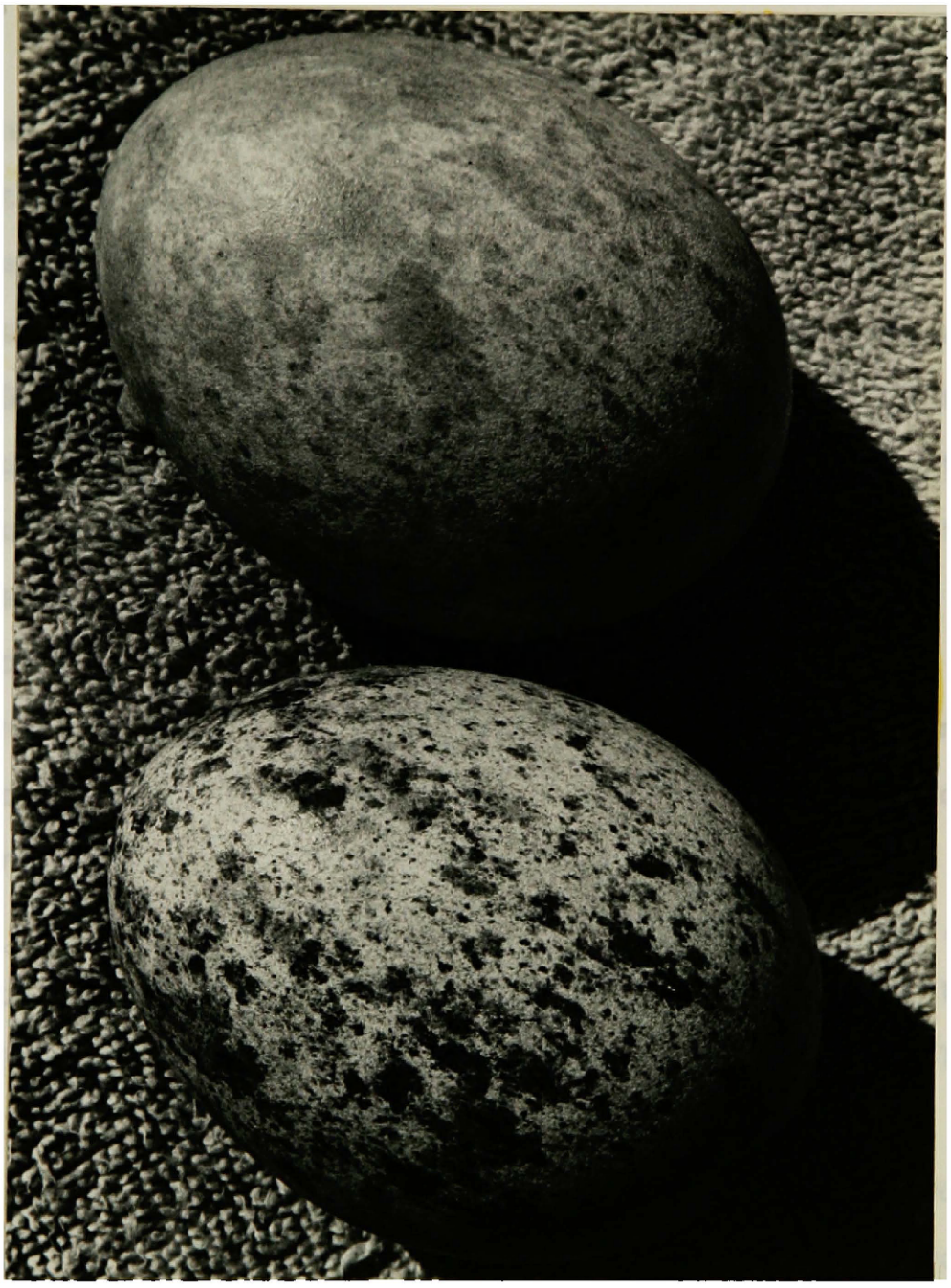
The males showed much interest in the female and in the eggs throughout the egg-laying period each year. The first time the female stood up after egg-laying, a male walked to the nest cup and peered down at the egg. He bent forward until his beak nearly touched the egg. Then, straightening up, he gingerly circled the egg, stopping several times to again stoop down. After

Table 2. Egg and incubation chronology.

Year	Date 1st egg laid & 2nd or 3rd egg observed	No. of egg	Approximate intervals between egg hours	Duration of intervals in days	Fertility	Disposition of Eggs
1973	22 March	1	0	52	Infertile	Removed from nest 5 May
1974	28 March	1	87-118	36	Infertile	Removed from nest 2 May (23 April)
	2 April	2			Intertile	Removed from nest 2 May
1975	22 March	1	96-112	57	Infertile	Egg broke in nest
	26 March	2			Infertile	Egg broke in nest
1976	27 March	1	95-97	28	Infertile	Removed from nest 28 March
	31 March	2			Infertile	Disappeared from nest
1977	22 March	1	168	38	Infertile	Removed from nest 28 April
	30 March	2			Infertile	Removed from nest 28 April
1978	30 March	1	0	46	Infertile	Removed from nest 9 April
1979	28 March	1	75-97	-	Infertile	Egg broke in nest 3 May
	1 April	2		-	Infertile	Disappeared from nest 17 May
1980	29 March	1		-	Fertile	Egg broke in nest 31 March
	13 April	2	*	41 - 44	Fertile	Egg hatched 27 May
	April	3	-	-	Fertile	Egg broke in nest 8 May

*Egg 2 is the first egg of the second clutch.

Figure 6. The first (bottom) and second (top) egg laid in the 1974 clutch.



this initial inspection, he settled down for his first bout of incubation.

Incubation

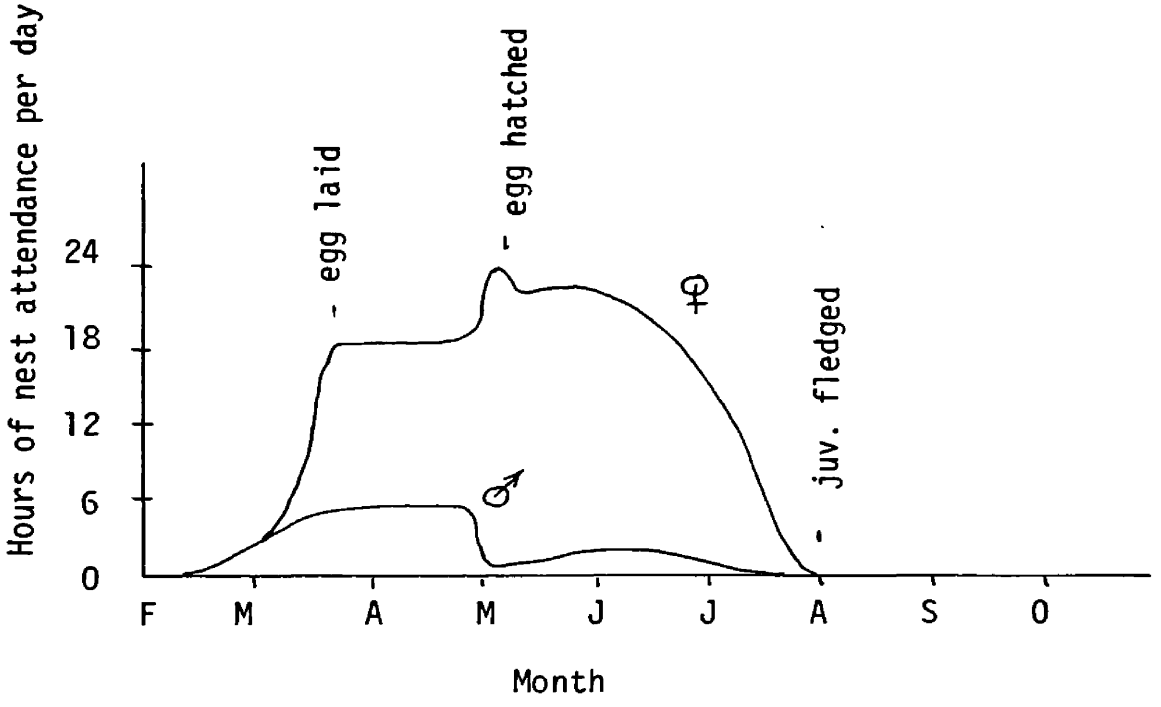
A general pattern of incubation was evident. The female began incubating as soon as the first egg was laid and was relieved by the male after 6-8 hours. The female always incubated during the 14-18 hours of dark. She left the nest in the early morning between 0600 and 0700 hrs for approximately one hour when she would stretch, defecate, and occasionally feed. The male immediately moved to the eggs and incubated. The timing of this early morning change varied little. Less predictable recesses occurred again during mid-day and late afternoon. The female usually fed during the afternoon recesses. These behaviors were quantified during the 1974 season. Each bird averaged four sessions per day (Table 3). The male had an incubation constancy (% of daylight hours on eggs) of 36% and the female, 64%. The female incubated throughout the night, however, making the total percent of incubation for the male 18% and for the female 82% (Fig. 7). The pair incubated their fertile egg for 41-44 days in 1980.

The settling behavior was the same in both sexes. A bird alighted on (or walked to) the edge of the nest and walked toward the clutch. As the eagle approached the clutch, it relaxed the feet, the toes curled inward forming a loose fist, and the ankles bent so the lateral surfaces of the feet bore the weight. As it moved closer to the clutch, it shifted the weight to the tarsi. If the

Table 3. Time eagles spent incubating as recorded on Rustrak Strip Chart per 24-hour period, 1974.

	Male	Female
Total length of session	4.3 hrs	19.7 hrs
Average length of session	1.0 hrs	5.5 hrs
Average length of bouts	.6 hrs	1.1 hrs

Figure 7. Golden eagle nest attendance in hours per day.


Hours of nest attendance per day
24
18
12
6
0
F
M
A
M
J
J
A
S
O
Month
- egg laid
- egg hatched
♀
♂
- juv. fledged

eagle was not yet over the clutch, it would take several crawling steps with its weight on the tarsi and the back at a 45^{o} angle. When it stopped directly over the clutch, the head pitched down between the legs, the beak sometimes touched an egg, and the eagle sometimes rolled an egg. As the eagle settled, it elevated its breast feathers and rocked from side to side. The eagles wings (which were held to the side) and beak touched the nest rim and appeared to bear some weight. Though the feet and legs were out of sight, it appeared that during the side rocking the eagle used its feet and legs to position the egg(s).

Once settled on the clutch, the eagle usually maintained an alert posture; it kept its head raised and looked around. Occasionally at night and during inclement weather the birds rested their heads on the nest in front of themselves and appeared to sleep.

While incubating, a bird often reached out and down, stabbed its beak into the nest material and then drew it back toward the breast ("beak stab," Ellis 1979). A bird also reached out and down with the head and pick up a particular stick or piece of vegetation between the mandibles. It would then yaw the head to either side and place the material on the nest. This rearrangement of material maintained a tight nest cavity and was perhaps important in preventing drafts from cooling the egg (Ellis 1979). The male often returned to the nest with a small stick or green vegetation in its beak and dropped it alongside, or sometimes on top of, the incubating female.

Egg Desertion

After an unsuccessful fostering experiment in 1974, an egg was returned to the nest and the pair incubated for an additional five days before deserting. The female was the first to show signs of disinterest. Three days before desertion, she left the egg unattended for an hour and a half. Two days before desertion, the female's incubation became brief and erratic and was less than 30% of normal. The male compensated by incubating during most of the female's recesses. One day before desertion, the female left the egg at 0030 hrs and did not return until 0600 hrs when she incubated for 15 hours. She did not return to the egg again. The male continued to incubate for the rest of that day, incubating during 15 bouts over an eight hour period. The following day the male performed three incubation bouts totalling 1.5 hours. The male then deserted the egg. During 1979, the pair incubated an egg for 61 days, or 39% longer than a normal incubation period. During the last days, the pair became less attentive. On the last day of incubation they left the egg exposed four times for periods of over an hour in cold rainy weather.

The male escaped from the aviary 12 hours before the female layed her first egg of 1980. On the first day of the male's absence, the female incubated continuously throughout the morning, but took a two-hour recess at 1400 hrs. On the second day the female incubated in several daylight bouts, but did not incubate during the night. On the third morning the female was observed removing egg shell fragments from the nest. The female remained on

the nest throughout the third night in egg-laying posture, but produced no egg. The male was returned to the aviary seven days following his escape, and the female began a second clutch nine days later.

Egg Hatching

Egg hatching was preceded by marked changes in adult behavior. On the day prior to egg hatching, 26 May 1980, I noted the following:

> "1030 hrs - the male has been more attentive this morning, making frequent trips to the nest.
> 1200 hrs - the male carried food to the nest, pulled a tiny piece off and offered it to the female. The female has been incubating in a more upright posture.
> 1300 hrs - the female frequently stands, shifts her posture and settles on the egg again."

When the pair incubated infertile eggs, none of the above behavioral changes were observed. Instead, the birds continued to incubate normally until they deserted the eggs. Shortly after egg-hatching or after an egg broke the female usually removed the large egg fragments by picking them up in her beak and carrying them to the edge of the nest platform.

Egg Incubation Temperatures

To determine incubation temperatures and the incubation effectiveness of the male and female, a temporal record of incubation temperatures, attendance and behavior was recorded on a Rustrak chart (Fig. 3). Temperature records for a seven day period in 1974 at the end of the incubation period revealed that the male and female

incubation result in nearly identical egg temperatures (Tables 4 and 5), and that they both were able to maintain a constant egg core temperature (Table 6).

Brooding Behavior

The telemetry egg was left in the nest cup for a three-day period after hatching during 1974 in an attempt to record and compare brooding temperatures. However, the adults responded to the telemetry egg as if it were an unhatched egg and their behavior was a combination of brooding and incubation. The male brooded 25% of the time and the female brooded 75% of the time during the three days (Table 7). Both sexes brooded at the same temperature (Table 8).

There was a definite change in the posture and behavior of the adults as their eaglets grew and the eaglets needs changed. On the first day following hatching, the adult posture on the nest was indistinguishable from that during incubation. By day two, the adult eagles no longer held their head in the same plane as their back, but held the head upright, with the heck at a right angle to the back. In this position, the eaglets could lay snuggled among the adults' breast feathers with their head exposed. As the eaglets grew in strength and began "squatting" (resting their weight on its tarsi and abdomen) rather than "laying" (resting its weight on its abdomen and chest), the adults accommodated by changing their posture. The adults raised their backs to an angle of 30-45 degrees and supported more of their weight on the tarsi. At three weeks of age, the eaglets began crawling out from underneath the brooding adult.

Table 4. Average temperature in degrees Centigrade at end of incubation bouts.

Thermistor Site	Bird Incubating	Range	Mean	σ	(n)
Core	M	30-34	32.8	.88	32
	F	29.5-35.5	32.8	1.23	87
Shell	M	31-35	33.6	1.12	32
	F	28-36	33.5	1.64	87

Table 5. Average temperature in degrees Centigrade at end of incubation sessions.

Thermistor Site	Bird Incubating	Range	Mean	σ	(n)
Core	M	30-34	32.5	1.06	15
	F	29.5-35	32.8	1.31	15
Shell	M	31-35	33.2	1.33	15
	F	30-35.5	33.5	1.44	15

Table 6. Mean temperature change per incubation bout in degrees Centigrade.

Thermistor Site	Bird Incubating	Range of Temperature Change	Mean	σ	(n)
Core	M	3.5	0	.58	32
	F	7	0	1.07	87
Shell	M	10.5	2.8	2.13	30
	F	7.5	2.9	1.65	86

Table 7. Time eagles spent brooding the telemetered egg per day post hatching.

	Male	Female
Average length of bouts	.5 hr	.8 hr
Average length of sessions	1.4 hrs	5.8 hrs
Total length of sessions	5.8 hrs	18.1 hrs

Table 8. Average temperature of telemetered egg in degrees Centigrade at end of brooding bouts during the post hatching period.

Thermistor Site	Bird Incubating	Range	Mean	σ	(n)
Core	M	32.5-34	33.5	.49	11
	F	32-35	33.5	.86	27
Shell	M	32-35	34.1	.85	11
	F	32.5-36	34.1	1.34	27

The adults usually shuffled along on their tarsi in pursuit. On bright, hot days, the adults sat upright and spread their wings (shading) which protected the young from intense sunlight. If fresh green vegetation was available during periods of intense heat, adults sometimes used it to cover the young. Brooding bouts became shorter and recesses more frequent as the eaglets grew older.

The male's interest in the hatching and newly hatched chick appeared high. This was particularly evident in male #2 during 1974 when a great horned owlet was fostered. The male was the first to approach the owlet and he settled down to brood for four hours, a period twice as long as his longest incubation bout and nearly four times as long as his average incubation bout. For the first time, the number of attentive sets for this male equaled those of his female.

Male #2 (1969-74) was much more active in parental care than was male #1 (1974-80). Following introduction of a foster eaglet in 1973, male #2 was more active initially than was his female, #7. He was first to brood, to refresh the nest with green boughs, to return to the nest with food, and the first to feed the foster eaglet. On the first day the eaglet was in the nest, the male performed four feeding bouts, while the female made only three. Over the years female #7 came to dominate all activities that occurred on the nest.

In the 1980 season, male #1 was the first to refresh the nest and to return to the nest with food on the day following hatching. His female, #7, however, was first to brood and to feed

the eaglet (Table 9). Though the male brooded three times for a total of 14 minutes on the first day, he did not feed the eaglet and was actually driven from the platform on a number of occasions by female #7.

Female #7 raised her first eaglet, a fosterling, in 1973. When the eaglet was 25 days old the female stood next to it, reached down with her beak, and began plucking its down feathers (pre-plumulae). These plucking bouts lasted from 1-4 minutes and occurred 4-10 times during the day; this apparently aberrant behavior lasted four days in 1973. The eaglet sat still for a short while and then tried to move out of reach of the female or to crawl beneath her. The plucking behavior occurred routinely in all subsequent years when an eaglet's feather tracts were just becoming visible under its pre-plumulae.

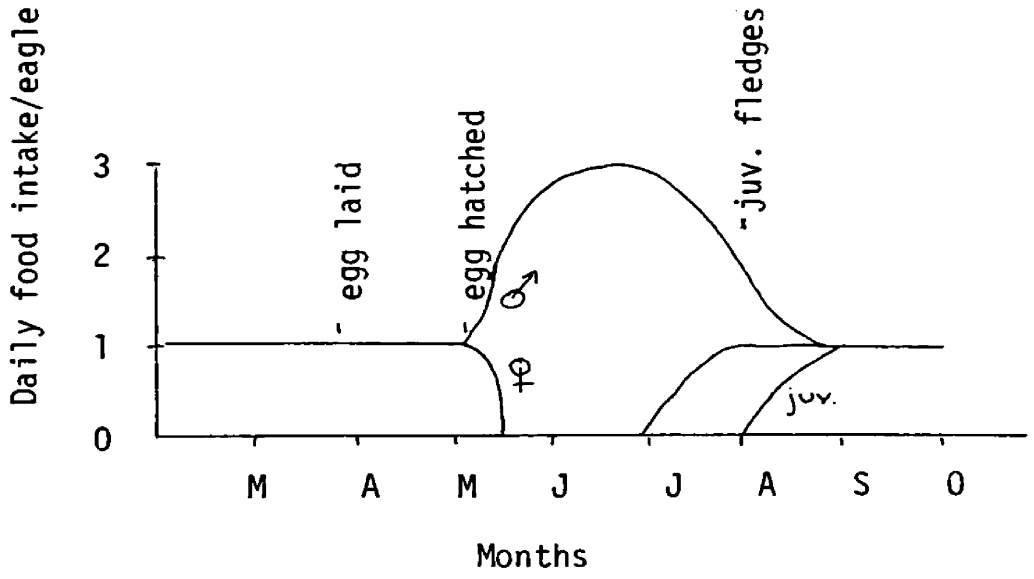
Food Gathering

Each year before hatching, both male and female eagles retrieved their own food from the aviary floor. The male only occasionally brought food to the incubating female. After hatching, and until the eaglets fledged, only the male retrieved food (Fig. 8). He carried ground squirrels to a perch underneath the nest where he plucked or skinned them and then carried them to the nest. The male never fed from the food during this time, but waited until late in the evening after both the female and young had fed. To test the rigidity of this behavior pattern I did not feed the eagles for two days. On the third day I placed an armful of green boughs and several ground squirrels in the aviary. The female stopped brooding

Table 9. Summary of which adult first performed specific behavior patterns after hatching or after foster chick was introduced into nest.

Year	First bird to: Brood	Return w/ food	Feed young	Refresh nest	Comments
1973	M	M	M	M	Brooded w/ during first 3 nights
1974	M	F	F	M	
1975	F	F	F	M	Male was absent from aviary for first two days after eaglet entered
1976	-	-	-	-	
1977	F	F M	F M	M	
1978	F	F M	F M	M	
1979	-	-	-	M	
1980	F	M	F	M	

Figure 8. The amount of food retrieved from the aviary floor by each eagle.


Daily food intake/eagle
3
2
1
0
egg laid
egg hatched
juv. fledges
♂
♀
juv.
M
A
M
J
J
A
S
O
Months

and flew to the boughs, and carried them to the nest. She ignored the food. However, the male flew to the squirrels, carried one to the perch, plucked it, and then carried it to the nest where he left it.

Feeding

The egg hatched during the night of 26-27 May 1980. At 0715 hrs, 27 May, the female arose from brooding for the first time. The eaglet's down was dry and its eyes were closed. The female fed the eaglet for the first time. On the first day the eaglet, apparently too weak to hold its head up, pitched its head back until it rested on the back and its bill pointed straight up. In this posture the eaglet accepted a morsel from the female and swallowed it. The eaglet's head then rolled and pitched down and forward to rest on the nest platform. This action pattern was repeated for each morsel offered. When the eaglet threw its head back, the female (the only parent to feed during this period) rotated her head very little or not at all. As the eaglet gained strength and began holding its head in a normal horizontal position during feeding bouts, the female assisted the young by lowering and rotating her head while offering morsels. By the end of the second day the eaglet was strong enough to hold its head up during feeding.

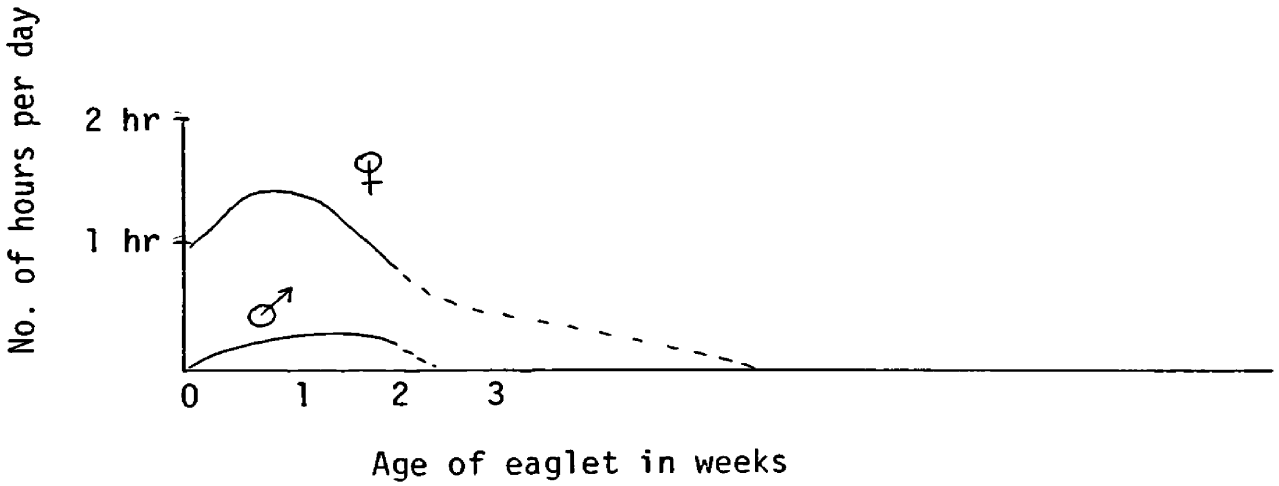
There were times each year just prior to egg-hatching and during eaglet rearing when an adult presented morsels to its mate. The mate did not always accept the proffered morsels. This behavior was first observed 24-36 hours prior to egg-hatching when the male

offered morsels to the incubating female. Shortly after hatching, the female offered morsels to the brooding male, who accepted them. The male sometimes offered morsels to the female when he was feeding a chick. The female accepted the morsels and then offered them to the eaglet who accepted and swallowed them.

Over a sample period of six days during the first month of parental care in 1980, the female fed the eaglet an average of 8.3 times (66 minutes total) per day and offered the eaglet an average of 25 morsels per feeding bout. The male fed or assisted in feeding the eaglet an average of 1.3 times (10 minutes total) per day, offering 17 morsels per bout (Fig. 9). The male not only spent less time feeding and fed less to the eaglet, but he was less adept in this behavior. During three feeding bouts when the male assisted the female, they both stood several steps from the eaglet tearing morsels from separate ground squirrels. As the female tore each morsel free, she took a step forward and offered it to the eaglet, the latter accepted it easily. The male failed repeatedly to take a step forward and, although both he and the eaglet stretched, they rarely succeeded in passing the food.

The male fed himself at dusk from food left in the nest. The female fed herself while feeding the eaglet. She consumed pieces which, when torn off, were too large for the eaglet to swallow. This general feeding pattern was observed each season.

Figure 9. Average time adults spent feeding young, 1980.


No. of hours per day
2 hr
1 hr
♀
♂
0
1
2
3
Age of eaglet in weeks

Nest and Territorial Defense

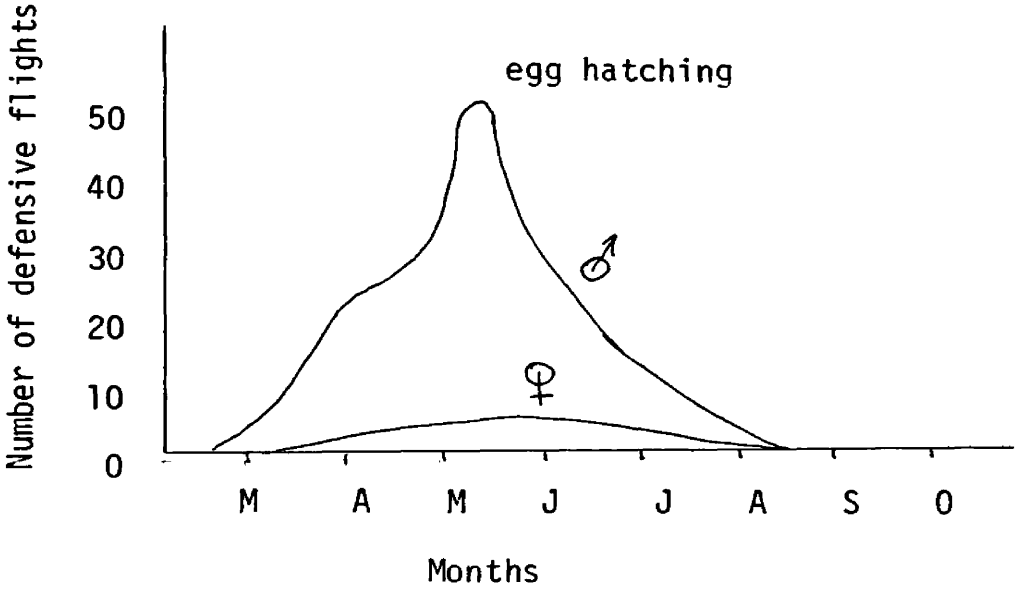
Nest and territorial defense are considered together because the eagles were confined to a small aviary where the distinction between these behaviors was usually impossible. At the extremes of aggressive behavior, some acts were clearly territorial defense, while others were for defense of the nest, e.g., both birds vocalizing at airplanes and large buteos flying overhead or both birds attacking and wounding an observer trying to visit their nest.

During the non-breeding seasons neither bird was aggressive toward non-eagle intruders. An observer could walk into the aviary and climb onto the nest platform without eliciting an attack. A strange eagle introduced into the aviary did, however, arouse aggressive behavior, especially from the male.

As the breeding seasons progressed, the male gradually became more defensive with an obvious increase in intensity at egg-laying. Twenty-four to thirty-six hours prior to egg-hatching, the male reached a peak in aggressiveness which declined slowly over the next six weeks. By the third month of parental care neither bird showed any aggression when an observer entered the aviary and handled their fledgling (Fig. 10).

The female's level of aggressive behavior more-or-less paralleled, but never reached the intensity of, the male's. At the time of hatching the male launched himself at the slightest sound or movement. In a one-day period, three weeks after hatching in 1980, the male made 27 defensive flights against the side of the aviary, while the female made one. Five weeks after hatching, the

Figure 10. Sex differences in aggression during the nesting cycle.


Number of defensive flights
50
40
30
20
10
0
egg hatching
♂
♀
M
A
M
J
J
A
S
O
Months

male made 9 defensive flights, while the female made none.

The eagles directed their aggression selectively towards specific groups and individuals. Unfamiliar people who approached to within 300 feet of the aviary elicited an attack by the male, while I and several others who were familiar to the eagle pair could move about quite freely. Only when we approached to within 30 feet would the male attack. Local dogs were allowed to walk near the aviary, usually receiving only a wary stare. Our family labrador, however, provoked instant action. The male flew against the aviary walls in the direction of the dog whenever he appeared at any distance. The female attacked when the dog approached within 30 feet of the aviary. Airplanes and large buteos were scolded when they flew overhead. However, the day after the eaglet hatched in 1980 a crow flew down to perch just above the aviary roof calling raucously. Neither bird paid it any attention, and the female even moved several feet from the eaglet leaving it exposed and vulnerable to a possible attack by the crow. Only when there was an imminent threat to the nest did the female become aggressive and attack except for her response to the family labrador described above.

On several occasions when it was necessary that an observer visit the nest, the pair made such an aggressive defense that the eaglet was injured by the adults. They abandoned their normally slow careful movement around the eaglet and failed to fold their feet and claws when they became motivated to attack the intruder.

During the course of the study the male escaped from the aviary three times during the nesting season. He escaped on the

52nd day of incubation on one occasion and 12 hours prior to egg-laying on another. In both instances he immediately left the nesting area entirely and was captured 7 days later approximately four miles away. The third escape by the male, however, occurred in 1980, 63 days after hatching. He stayed within 200 m of the aviary for the entire four days of his sojourn. The female scolded and the eaglet gave food-soliciting calls whenever the male was in sight. The male had not been fed for 1.5 days prior to his escape and was not fed during the four-day absence. Ten birds of various species, viz., six canada geese (Branta canadensis), one domestic goose (Anser sp.), two golden eagles, and one rough-legged hawk (Buteo lagopus), were tethered or caged 10-30 m from the aviary. The male neither attacked the golden eagles as territorial intruders, nor the hawk or geese as prey species. In the first three days of the male's absence, the female (for the first time during the 1980 nesting season) retrieved food from the aviary floor to the nest. On the fourth morning of the male's absence, food was placed just inside the aviary door. Within minutes, the male flew through the open door, grabbed the meat and, without stopping, carried it to the nest and dropped it in front of the eaglet.

Fostering and Cross-fostering

Between 1973 and 1979, the female eagle produced 12 eggs, but none were fertile. To allow the eagles to carry the nesting cycle to completion each year, a program of fostering and cross-fostering was adopted (Table 10). This technique was used to allow

Table 10. Fostering schedule for golden eagles.

Year	Species fostered	Date entered into nest	Disposition of fosterlings
1973	1 golden eaglet	5 May	Released after fledging 19 June
1974	1 great horned owlet	23 April	Removed from nest 26 April
1975	1 golden eagle egg 1 golden eaglet	29 April 17 May	Egg failed to hatch Released after fledging
1976	2 red-tailed hawks	23 April	Released after fledging
1977	1 golden eaglet	28 April	Remains in captivity 1980
1978	2 red-tailed hawk eggs	9 May	Hatched 12 and 14 May, released after fledging
1979	1 red-tailed hawk egg	9 May	Egg removed 28 May, adled

the adults to gain parental experience and to provide observations of parental behavior.

Although the pair did not copulate successfully in 1973, they performed all behaviors necessary to raise and fledge a two-week-old foster eaglet.

The pair did experience some difficulty during the first week in adjusting their behavior to accommodate the older chick. Initially, the male and female fed the eaglet very small morsels at 4-6 second intervals, and fed only a total of 6-15 morsels in a feeding bout. This feeding schedule, though appropriate for a 1-7 day eaglet, was inadequate for a two-week eaglet. Fortunately, the adults were able to adjust to the older eaglet's needs within 3-4 days. In 1974, a 14-day-old great horned owl was substituted for two infertile eggs. This was done before termination of the normal 44-day incubation period. The owlet was substituted on the 26th day of incubation. A telemetry egg was also placed in the nest cup for 36 hours to record brooding temperatures. Both birds accepted the owlet immediately but appeared confused. The male was the first to brood. Later he alternated with the female. The presence of the owlet stimulated the female to bring food to the nest, but no attempt was made to feed the owlet the first day. On the second day, the female made several attempts to feed the owlet with little success. The owlet's response to the female's offer of food was to sit or lay prone. From this position it stretched its neck up, rolled its head back, opened its mouth and emitted hunger "cheeps." The female offered the owlet very tiny morsels of flesh using a feeding posture

suitable for a newly hatched eaglet. This resulted in food being presented at the base of the owlet's neck. The owlet received only one morsel from a number offered that day. At times, the owlet wandered 1-2 m from the adults in search of food and tried to feed itself from a carcass. Because the adults' primary concern continued to be the unhatched egg, it was removed at 2020 hours on the second day. However, the adults continued to lay over the nest cup in an incubation posture. They remained tolerant of the owlet, brooding it whenever it approached closely, but were unreceptive to its solicitations for food. On the third day the female made three successful feeding attempts, but the owlet was not fed on the fourth day. It then tried to feed itself from a carcass, but the female pulled the carcass out of reach. This interaction continued for five minutes. During the second and third night the owlet was brooded only when it inadvertently clambered into the nest pocket. The brooding bouts were short. On the fourth day, the owlet was removed from the nest. From feeding experiments conducted with the owlet prior to and after removing it from the nest it appeared that a visual-tactile rather than an auditory-visual cue was necessary for the owlet to respond. When portions of mice were offered and then allowed to lightly touch the owlets beak or cere, it responded by opening its mouth and receiving the proffered food. Normally the owlet raised its head back, closed its eyes and groped for the food particle until it made contact with its beak. I concluded that the adults were unable to alter their inherent parental behavior to

provide the alien feeding cue and accommodate to the advanced developmental stage of the horned owl chick. They attempted to attend the precocial owlet with behavioral patterns appropriate to a 1-3 day old eaglet. The adults had no trouble adjusting to foster eagle chicks in 1976-1978, despite the introduction of male #1, a new and inexperienced parent in 1976. In each of these years the chicks, less than one week old, were introduced after the normal incubation period when their developmental stage was in phase with the adults behavioral patterns.

There was no distinguishable difference in the parental care given fostered red-tailed hawks and golden eaglets. Though in other circumstances the red-tailed hawk would be treated as a prey species by golden eagles, the fosterlings were treated as conspecifics, even after they were fledged and free to fly around the aviary.

CHAPTER IV

DISCUSSION

This study of courtship, nest construction, incubation, and parental behavior of captive golden eagles answers some questions on their breeding biology and behavior, and poses others concerning the requirements for successful propagation of captive eagles.

Courtship or territorial display flights (impossible in the aviary) apparently were not a requirement for pair formation or for synchronizing nesting behavior. Perching close together or side-by-side, "mutual roosting," is reported to be the earliest indication of "successful pair bonding" in peregrine falcons (Falco peregrinus) and American kestrels (Falco sparverius) (Cade 1960, Olendorff 1968). My captive golden eagles exhibited mutual roosting from the first year they were together, but took six years to copulate successfully. A pair of golden eagles at the Topeka Zoo did not produce fertile eggs until three years after pairing was first observed (Steenburg 1978). However, one pair of captive golden eagles produced fertile eggs after being together for only one season (Voelker 1980, pers. comm.). A pair of captive bald eagles did not produce fertile eggs until their third season together (Maestrelli and Wiemeyer 1975). Wild eagles on a nesting territory may produce fertile eggs in less time than do captive eagles; however, field studies on marked individuals of known age are needed to confirm this.

Golden eagles are considered mature at three to four years

(Brown and Amadon 1968). However, golden eagles in subadult plumage have nested successfully and raised young (Bates 1976, Sandeman 1957 in Newton 1977). Throughout the nesting season the captive female was aggressive and the male submissive, deferring to the female in many situations. A well intergrated pair-bond, insuring successful copulation may require a fine balance between female aggression and male appeasement behavior. The captive eagles strengthened the bond between them over a period of years. This probably resulted from the successful completion of successive nesting cycles. This study indicates that the crucial aspect of breeding captive golden eagles in captivity is the formation of a pair bond which is sufficient to insure successful copulation. Pair formation of this type may require 1-6 years.

The two pairs of captive golden eagles observed in this study used the same basic nesting strategy reported for wild pairs (Craighead 1967, McGahan 1968, Reynolds 1968, Camenzind 1968, Ellis 1973, and Beecham 1975). The average number of eggs laid annually by the female during the eight years of this study was 1.88. This compares favorably with data from wild populations: 2.10 eggs reported by McGahan (1968), 1.91 by Camerzind (1969), 2.1 by Beecham and Kochert (1975), and 1.61 by Olendorff (1973). In contrast, eagles at Topeka Zoo consistantly produced three eggs per clutch except during 1970 and 1975 when they produced five eggs and two eggs, respectively.

The interval between laying of the first and second eggs was approximately 36 hours. This differs from intervals of up to one

week reported by Oberholster (1906), three to four days reported by Gorden (1955), and a three-day interval averaged over a seven-year period for a pair of captive golden eagles at Topeka Zoo (Steenburg 1978).

The eagle pair incubated their fertile egg for 41-44 days in 1980. The average incubation period for eggs hatched at the Topeka Zoo from 1971 through 1976 was 41 days. Other literature shows the normal incubation period for golden eagles to be 43-45 days (Gorden 1955).

Incubation temperatures were telemetrically recorded for a wild eagle by Ellis and Varney (1973). Using identical equipment, I recorded core and shell temperature highs of 35.3 C and 36.0 C, respectively. This compares favorably with the temperature highs of 38 C and 40 C for core and shell recorded by Ellis and Varney (1973). They also reported egg core and shell incubation temperature lows of 11 C coincident with a nine-hour absence of the female. The lowest temperatures I recorded were 29.5 C and 28 C for the core and shell, respectively. The range between core temperature extremes was 27 C for eggs in the wild nest, but only 6 C for eggs of the captive eagles. The nine-hour absence of the wild adults may have represented response to an unusual disturbance near the nest or a prolonged period of hunting. Such as absence during inclement weather could be lethal for the eggs. The longest break in incubation recorded for my captive birds was approximately five minutes.

The captive male golden eagles in this study maintained the same egg core temperature as did the female. This is of obvious survival value for the embryo in time of acute food shortage.

In the peregrine falcon, the role of the sexes during incubation is related to size dimorphism and to egg size. The female falcon performs most of the incubation because the males' smaller size makes him less efficient at incubating the clutch (Nelson 1970). This reasoning does not apply to the golden eagle which has fewer eggs per clutch and eggs which are smaller in relation to body size. The peregrine falcon egg is approximately 5.3 percent of female body weight, and clutch size is 3-4 eggs (Nelson 1972, Walpole-Bond 1938). The golden eagle egg is 3.0 percent of female body weight and clutch size is only two eggs (Gorden 1955). Wild male golden eagles share incubation with the female. However, the proportion of incubation performed by males is not known for wild birds. One of my captive males accounted for an average of 18 percent of the total incubation time.

The male eagles did not bring food to the incubating female in my study but incubated the eggs while she ate her meal. Among wild eagles, the female does little or no hunting during the incubation period. The male makes the kill, then transfers prey to the female at some distance from the nest. The female is strongly motivated to remain on the eggs during incubation. It is important for a large predatory bird to maintain its muscle tone. It may be that the male pattern of not feeding the incubating female is a necessary incentive for her to leave the nest and

exercise. This behavior also shortens the period during which food is at the nest, and reduces the chance of pest contamination or of other predators being attracted to the nest.

Brooding temperatures averaged 0.7 C higher than incubating temperatures. This increase could have been caused by a change in body temperature in the adults after egg hatching, by a change in the attentiveness of the brooding adults, or by an increase in temperature associated with increased metabolism of the newly-hatched chick.

Over a period of eight nesting seasons, the male deserted the nesting effort twice: once before egg laying and once during incubation. The female deserted once during incubation. Neither bird deserted after hatching when both sexes were highly motivated to attend the young.

It has been reported that male golden eagles regularly brood the young (Brown and Amadon 1968). Both parents were observed to brood young at the Topeka Zoo (Steensburg 1978). In my study the males also brooded. However, efforts varied between the two males, and from year to year for each, and the overall efforts of both were minimal compared to those of the female.

It would appear that the male golden eagle has developed the necessary physiological and behavioral traits to incubate as efficiently as the female, but exhibits poorly developed parental care abilities. This may be explained by the male's hunting role, especially following hatching. Fully occupied with food procurement, he has not evolved parental care abilities to match those of the female.

The females' plucking of down from the eaglet is probably aberrant behavior caused by confinement at a time when she would be increasingly active procuring food in the wild. At times, it appeared uncomfortable to the eaglet, but it caused no apparent damage. This behavior is not described in the literature for birds in the wild.

Fifteen golden eagle chicks were hatched at the Topeka Zoo from 1971 to 1976. Eight of the chicks died of traumatic injury, inadequate food intake, or disease before fledging. The birds in my study fledged four eaglets and four red-tailed hawks with no fatalities. An adequate diet is essential for normal development and sustained growth of eagle chicks. A commercially prepared food, Zu/Preem Birds of Prey Diet proved adequate at Topeka (Steenburg 1978). I found lean beef, horse meat or fresh chicken to be an adequate diet prior to active nest building. After that time, freshly killed ground squirrels supplemented with lean meat kept both adults and young healthy.

In the wild, golden eagles do not defend their nests against man, as many other raptors do (Craighead 1969). The female golden eagle at the Topeka Zoo exhibited extreme defensive behavior, but the male showed none (Steenburg 1978). This is the reverse of what I found and may be related to the individual birds' social experience with man. My captive eagles defended so vigorously that they struck human intruders. Their defense behavior could be characterized as frenzied. On several occasions they inadvertently injured their eaglet and once broke an egg in aggressive defense

activity. Socialization with man apparently lowered the aggression threshold while raising that for fear. This produced frequent and intensive displays of man-directed aggression during the nesting season. Similar aggressive behavior was directed toward any unusual intruder during the nesting season.

Golden eagles readily accepted and tried to raise young of other species placed in their nest. Pet golden eagles have raised broods of great horned owls, ducks, geese, and red-tailed hawks (Durdent 1972, Hamerstrom 1970). In the present study, eagles fostered a great horned owl and two broods of red-tailed hawks. The eagles not only raised non-specific fosterlings, but behaved toward them as if they were con-specifics, even after fledging. All of the above mentioned species are normal prey for the eagle. It would be interesting to determine at what point the eagles would distinguish between an offspring and a potential food item, and the physical or behavioral characteristics adults use to identify their foster offspring.

As a predator at the top of the food chain the golden eagle must exploit a specialized and unpredictable food source (Odum 1959, Grossman and Hamlet 1964). Both sexes share in the nesting effort, thereby avoiding stress that would accure to a single member of the pair performing all nesting duties. As environmental and physiological variables changed throughout the nesting season, and from season to season, the male and female eagles maintained a dynamic equilibrium in their respective nesting activities and were

flexible in meeting changing needs. The female however, seemed more rigidly programmed. Much of the males' nesting behavior was less well defined and was initiated by cues from the female. He characteristically responded positively to alterations in the usual routine of nesting. This flexibility in male behavior could be crucial for the pair in overcoming adversity and unusual circumstances during nesting. For example, in performing 90 percent of nest construction, the male may have been compensating for the wing injury which impared the females' ability to carry sticks to the nest. The addition of greenery continued throughout the parental care period and served three functions. The boughs created a cool nest environment during hot days. They broke and deflected chilling winds, and they covered soiled nest material. The males' incubation bouts were initiated by the female leaving the nest pocket and exposing the eggs. A bout ended when the female approached the incubating male, sometimes nudging him with her beak. When infertile eggs were deserted the female deserted first; the male tried to compensate for her absences by incubating 30 percent longer than normal. Thus, female determined the onset and length of incubation sessions, while the male filled in for her. Both male #1 and male #2 participated more in parental care during early years when the female appeared less competent.

Every organism tries to survive. Raptors survive by killing other species which, for golden eagles includes a wide range of prey. During the non-nesting season, the hunting role predominates for

both sexes with some cooperative hunting occurring among paired adults. If one assumes that procurement of food is the single most powerful self-interest drive for survival of the individual, then the nesting cycle can be viewed as a period when the self-interest motivation is ameliorated by "altruistic" behavior. In an annual time frame, the entire reproductive cycle can be considered as a period of "altruistic" behavior in which the female largely negates her immediate self-interests (procuring food) and diverts her energies to reproducing. For about 80 days she is largely dependent on the male for securing her food. The male compromises his basically selfish behavior to the extent that he shares his kill early in the nesting cycle with the "nest bound" female and later in the cycle, with both female and young. Viewed in an evolutionary time frame, the nesting season must be considered as non-altruistic behavior. But viewed in the much shorter annual time trame, the individual overt behaviors of both male and female appear to have altruistic implications.

As the nesting season proceeds, the pair cooperates in many activities; nest building, incubation, and care of young. They share, but not equally, in these activities. The male's role remains predominately that of hunter and food supplier and the female's role that of attending egg and young. During incubation and the first few weeks of chick care, the female's most vital function is to provide protection and a source of heat for the developing eaglet. As the eaglet grows the female is gradually freed from nest-oriented parental duties, resumes the hunting role,

and helps meet the increasing nutritional needs of the young. The parental role wanes rapidly at fledging. Finally, the primary activity of both adults and full-grown eaglets is to procure their own food. The hunting role predominates in both adult sexes for approximately seven months until a new nesting cycle begins. For the eaglets the role of hunting will predominate for four to six years until they form a pair-bond and begin nesting.

CHAPTER V

SUMMARY

Sexual differences during courtship, nest construction, incubation, and parental care of captive golden eagles were studied. Nest building activities were observed first in February. Copulation took place during March. Eggs were laid at the end of March and in early April. Usually two eggs were laid, approximately 36 hours apart. The incubation period was approximately 44 days, and the fledging period 65-70 days. Pair bonding behavior was subtle and occurred over a six-month period prior to nest construction. The male was responsible for 90% of nest construction, but the female was active in forming the nest cup. The female incubated 82% of the time. During the incubation period the male brought green boughs to refreshen the nest. The male escaped from the aviary twice during incubation. Both times he deserted the area. After the eggs hatched the male brought all the food to the nest for the female and the young. The male escaped from the aviary once after hatching but remained close and returned to the aviary and nest on his own volition. Throughout the nesting period the male actively tried to defend the aviary from intruders (i.e., people and dogs which walked near by and hawks and airplanes which flew overhead). His aggressiveness peaked just after egg hatching. The female defended only when the nest platform was threatened.

The pair was successful at fostering eaglets and red-tailed hawks, but were unsuccessful with a great horned owl.

A review of the literature indicates that only at the Topeka Zoological Park, Topeka, Kansas (Steenburg 1978) and Bill Voelker (pers. comm.) have succeeded in breeding and raising golden eagles in captivity prior to this study.

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